Z. Säugetierkunde **62** (1997) 99–107

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Geographic variation and divergence in nonmetric cranial traits of *Arvicola* (Mammalia, Rodentia) in southwestern Europe

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Receipt of Ms. 00. 00. 1996
Acceptance of Ms. 00. 00. 1996

Abstract

Geographic variation and divergence of 21 nonmetric cranial traits were studied in six samples of water voles from southwestern Europe (*Arvicola terrestris*: southeastern and western Switzerland, French Massif Central, Spanish Pyrenees and northwestern Spain; *Arvicola sapidus*: Ebro Delta, Spain). Phenetic distance among samples was expressed by the mean measure of divergence (MMD) obtained from the transformation of the trait frequencies into angular values. From the MMDs of each sample, a cluster analysis was performed by the unweighted pair-group method using arithmetic averages (UPGMA). In the distance phenogram all samples of *A. terrestris* formed a cluster separated from *A. sapidus*. Among the former, the sample from southeastern Switzerland showed maximal phenetic differentiation against the remaining samples. The degree of phenetic divergence between the Iberian samples is higher than that between specimens from northwestern Spain and those from the Massif Central and western Switzerland. The lowest differentiation was observed between the samples from the Massif Central and western Switzerland. Since these results agree, in general terms, with our current understanding of the morphological, biometric, biochemical and reproductive relationships among several of the populations studied, nonmetric cranial traits can be considered useful for the evaluation of genetic differences in *Arvicola*. Under this assumption, taking into account the results obtained corresponding to the French and Spanish samples analysed, new considerations about the genetic relationships of central France, Pyrenean and northwestern Spain populations of *A. terrestris* are presented.

Introduction

Water voles of the Palaearctic genus *Arvicola* includes two species, which are recognised on the basis of morphological (Heim de Balsac and Guislain 1955), biometric (Reichstein 1963), cytogenetic (Matthey 1955, 1956; Díaz de la Guardia and Pretel 1979; Burgos et al. 1988) and biochemical characteristics (Graf and Scholl 1975; Graf 1982; Saucy et al. 1994): the southwestern water vole, *A. sapidus*, and the northern water vole, *A. terrestris*. The former is a semiaquatic rodent that occupies the Iberian Peninsula and much of France (cf. Reichstein 1982; Baudoin 1984). The northern water vole extends almost continuously throughout the northern Palaearctic region (cf. Corbet 1978) and shows two ecological forms: the fossorial and the semiaquatic (see e. g. Morel 1981). In southwestern Europe, where both species can be sympatric (Fig. 1), *A. terrestris* shows discontinuities in its distributional area (cf. Morel 1981; Baudoin 1984; Castién 1984; Álvarez et al. 1985; Ventura and Gosálbez 1988; Castién and Gosálbez 1993/94), which are associated with morphological, biometric and biochemical differences among several geographic populations (cf. Heim de Balsac and Guislain 1955; Reichstein 1963; Corbet et al. 1970; Engels 1975; Graf 1982; Ventura and Gosálbez 1989; Ventura 1991; Saucy et al. 1994).

Fig. 1. Geographic distribution of *Arvicola* in southwestern Europa (cf. Morel 1981; Baudoin 1984; Castién 1984; Álvarez et al. 1985; Ventura and Gosálbez 1988; Borghi et al. 1991; Castién and Gosálbez 1993/94). *A. sapidus*: horizontal lines; *A. terrestris*: vertical lines (fossorial form: widely spaced lines; semiaquatic form: densely spaced lines). Origin of the samples analysed: 1: Lugano; 2: Nyon; 3: Ally; 4: Ribadesella; 5: Aran Valley; 6: Ebro Delta.

Variation in frequency of minor skeletal variants, known as nonmetric traits, are useful for assessing population variation in time and space as the result of genetic relationships (for theoretical considerations, see e.g. Howe and Parsons 1967; Berry and Jakobson 1975; Sjøvold 1977; Hauser and de Stefano 1989; McLellan and Finnegan 1990). In rodents, particularly, results obtained from the analysis of sets of nonmetric variants have been frequently used to evaluate genetic divergence among populations (e.g. Berry 1963; Berry and Searle 1963; Berry and Jakobson 1975; Patton et al. 1975; Berry et al. 1978; Hartman 1980; Sikorski 1982; Kryštufek 1990; McLellan and Finnegan 1990). To our knowledge only the study by Corbet et al. (1970) deals with the geographic variation of nonmetric characters in *Arvicola*; the incidence of nonmetric cranial traits in several European populations was used, together with biometric data, to elucidate the taxonomic status of British water voles.

The main goal of the present study is to determine the geographic variation of the frequencies of nonmetric cranial traits in several southwestern populations of *Arvicola*, and to evaluate the usefulness of these variants in systematic studies in this genus. A further aim of this study is to frame the genetic relationships among several Iberian and French populations of the northern water vole using nonmetric cranial variants. Although some of our specimens come from the same geographic regions as those surveyed by Corbet et al. (1970), we have grouped them differently, reflecting the taxonomic changes appearing after that study. Likewise, we have introduced further theoretical considerations established after the study by Corbet et al. (1970), to process nonmetric trait frequencies (cf. Green et al. 1979; Hartman 1980; Andersen and Wiig 1982).

Material and methods

The material analysed consisted of 259 skulls of adult specimens of *Arvicola* from the following six geographic samples, which are stored in the collection of the Department of Animal Biology (Vertebrates) at the University of Barcelona (Fig. 1): 33 from Lugano, Ticino, Switzerland (*A. t. italicus*), from July 1993; 21 from Nyon, Vaud, Switzerland (*A. t. scherman*), from June 1993; 60 from Ally, Massif Central, France (*A. t. scherman*), from July 1983; 54 from Ribadesella, Asturias, Spain (*A. t. cantabriae*), from July and August 1984; 55 from the Aran Valley, Lérida, Spanish Pyrenees (*A. t. monticola*), from July and August 1983; 36 from the Ebro Delta, Tarragona, Spain (*A. sapidus*), from 1983 and 1984. In contrast to the study by Corbet et al. (1970), we have grouped the individuals coming from the south (Lugano) and the north of the Alps (Nyon) in independent samples, since the semiaquatic animals from canton Ticino (Switzerland) show significant biochemical differences (Graf 1982) and mechanisms of reproductive isolation from the nearest fossorial populations from the north of the Alps (Morel 1981). Specimens from the Massif Central were also considered independently, in order to determine the degree of phenetic differentiation against the populations from Switzerland and Spain. Because of the significant biometric and morphological differences found between the Pyrenean (Aran Valley) and Cantabrian (Ribadesella) *A. terrestris* (Engels 1975; Ventura and Gosálbez 1989; Ventura 1991), specimens from those regions were also considered separately.

Twenty-one nonmetric traits were scored on the skull and mandible; sixteen were foramina and five were sutures or variations of the morphology of particular skull bones. All these characters were coded as discrete variables (present or absent; single or double). The following traits were considered (Fig. 2; definitions appear only in those traits not previously referred to in the literature or modified for *Arvicola* from other species): 1. Fused nasals; 2. Preorbital foramen double; 3. Anterior frontal foramen present; 4. Posterior frontal foramen double; 5. Frontal suture present: the posterior portion of the frontal suture is present; 6. Wormian bones present; 7. Interparietal bones not fused; 8. Foramen incisivum single; 9. Maxillary foramen I present; 10. Maxillary foramen II (lateral) present; 11. Palatal hollow: the posterior border of the palatine bone is bent forwards forming an arch; 12. Foramen sphenoidale laterale ventrale present; 13. Foramen sphenoidale medium present; 14. Basioccipital foramen present; 15. Foramen hypoglossi double; 16. Ethmoid foramen double; 17. Foramen ovale double; 18. Foramen infra-ovale absent; 19. Supra-dentary foramen present; 20. Mental foramen double; 21. Mandibular foramen double. All skulls used in this study were scored by the same person (MASF) in order to avoid inter-observer errors.

Several of the traits examined (2, 10, 12 and 21) showed more than two states (absent, single, double, triple, etc.). In order to obtain a simpler situation for comparative purposes (cf. Andersen and Wiig 1982), these particular traits were artificially dichotomized, and scored as absent or present (traits 10 and 12), or single or multiple (double, triple, etc.), in which case the trait was scored as double (traits 2 and 21). Since several skulls were damaged, the frequency of some traits was based on a lower number of specimens than the total sample size. Since every species possesses a characteristic set of minor skeletal traits (Sjøvold 1977), we used most of the variants examined in *Arvicola* by Corbet et al. (1970) and defined by Berry and Searle (1963; traits 2, 3, 4, 9, 10, 13, 14, 15, 17 and 20); likewise other variants used in other species (Bateman 1954: trait 8; Berry 1963: traits 12 and 21; Sikorski 1982: traits 1, 6, 7, 16 and 19) and other new variants for this genus (traits 5, 11 and 18) were analysed.

The percentage of occurrence of each trait was noted for all samples examined. Bilateral variants were scored on the right and left sides separately, and trait frequencies were calculated taking into account the total number of sides examined (for theoretical considerations, see Green et al. 1979). A nonmetric chi-squared test was used to evaluate the differences between sexes. Only those traits that differed significantly between at least two of the samples were used for comparative analyses (test $X^2 \geq 3.84$, $p \leq 0.05$; Andersen and Wiig 1982). In order to stabilize the variance (cf. Hartman 1980; McLellan and Finnegan 1990), the incidence of each character was transformed into angular values following Freeman and Tukey (1950; see also Sjøvold 1973; Green and Suchey 1976; Green et al. 1979). From these data, genetic differences between two samples were tested using C. A. B. Smith's mean measure of divergence (MMD), following Green et al. (1979). Statistical significance of the differences between two samples was tested by the standard deviation of MMD (Andersen and Wiig 1982; Sikorski 1982). The degree of divergence of one sample from the others was expressed by the measure of uniqueness (MU), which was calculated as the sum of the MMDs of each sample (Andersen and Wiig 1982). Based on the MMDs a phenogram was constructed by the unweighted pair-group method (UPGMA; Sneath and Sokal 1973) using arithmetical averages on the correlation matrix. A phenogram was constructed using the routines SAHN and TREE of the Numerical Taxonomy System of Multivariate Statistical Programs (NTSYS-pc; Rohlf 1994).

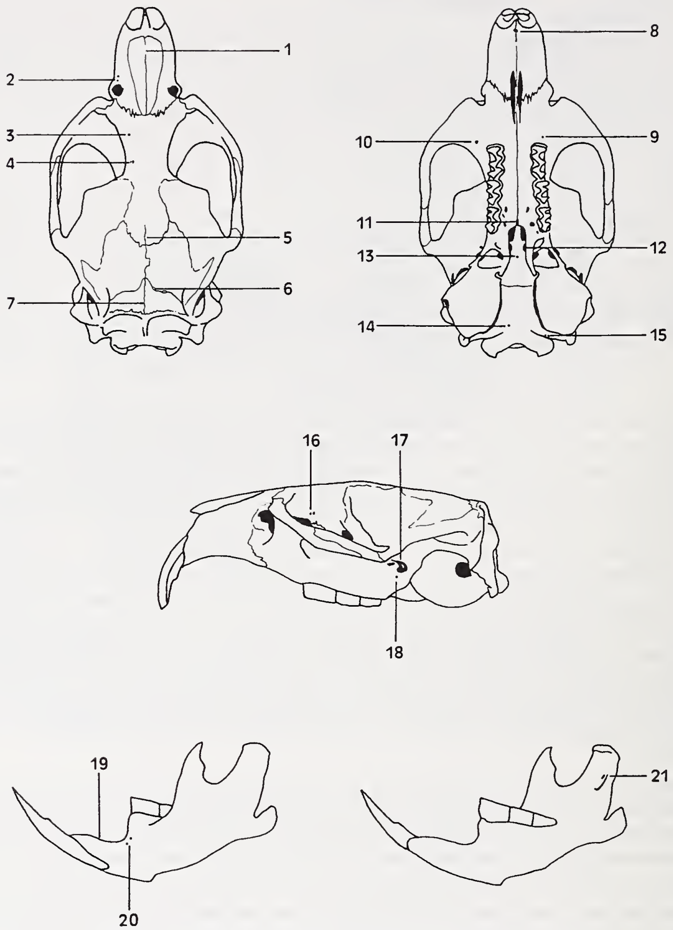

Fig. 2. Nonmetric cranial traits analysed in *Arvicola*.

Results

No significant difference between sexes was observed in the occurrence of cranial nonmetric traits in any sample, thus interpopulation analyses were performed using the combined frequencies for males and females (Tab. 1). Traits 15 and 19 did not differ significantly among samples. The frequent multiple division of trait 2 determined, in some cases, an arbitrary dichotomization of the character. Likewise, traits 1, 4 and 18 were sometimes very difficult to score. Comparisons of single trait incidence among samples indicated noticeable geographic variations in several cases, especially in traits 5, 8, 11, 13 and 21 (Tab. 1).

To compute phenetic divergence between pairs of samples the following 15 traits were considered: 3, 5–14, 16, 17, 20 and 21. The standard deviations of the MMDs obtained for these traits revealed that, except for the comparison between the samples from Nyon and Ally, all the phenetic distances among geographic samples were significant (Tab. 2). The

Table 1. Frequencies of 21 nonmetric cranial traits in six populations of *Arvicola* from southwestern Europe. *A. terrestris*: Lugano, Nyon, Ally, Ribadesella and Aran Valley; *A. sapidus*: Ebro Delta. k: trait occurrence; n: number of sides examined; %: percentage of trait occurrence.

Trait	Lugano		Nyon		Ally		Ribadesella		Aran Valley		Ebro Delta	
	k/n	%	k/n	%	k/n	%	k/n	%	k/n	%	k/n	%
1	27/33	81.8	19/21	90.5	47/56	83.9	9/47	19.1	46/54	85.2	23/35	65.7
2	7/64	10.9	7/41	17.1	28/107	26.2	52/96	54.2	8/106	7.5	8/71	11.3
3	1/66	1.5	2/41	4.9	13/93	14.0	11/92	12.0	6/110	5.4	2/72	2.8
4	5/66	7.6	6/42	14.3	6/75	8.0	11/94	11.7	0/110	0	0/72	0
5	18/33	54.5	3/21	14.3	5/48	10.4	2/50	4.0	0/55	0	5/36	13.9
6	0/66	0	0/42	0	2/89	2.2	1/98	1.0	0/110	0	9/69	13.0
7	0/33	0	0/21	0	2/48	4.2	0/49	0	0/55	0	5/36	13.9
8	11/33	33.3	14/21	66.7	42/60	70.0	39/48	81.2	43/54	79.6	19/36	52.8
9	30/66	45.4	14/42	33.3	31/115	27.0	20/97	20.6	38/110	34.5	35/72	48.6
10	41/65	63.1	37/42	88.1	97/111	87.4	85/98	86.7	92/110	83.6	70/72	97.2
11	29/33	87.9	18/21	85.7	32/58	55.2	23/52	44.2	51/55	92.7	24/36	66.7
12	46/57	80.7	39/42	92.9	44/57	77.2	71/87	81.6	61/106	57.5	70/70	100
13	8/33	24.2	1/21	4.8	2/39	5.1	20/48	41.7	4/55	7.3	36/36	100
14	0/66	0	1/42	2.4	11/84	13.1	8/98	8.2	19/110	17.3	15/72	20.8
15	65/66	98.5	40/42	95.2	85/85	100	98/98	100	109/110	99.1	71/71	100
16	10/66	15.1	1/42	2.4	1/87	1.1	0/96	0	6/110	5.4	4/72	5.6
17	66/66	100	41/42	97.6	77/81	95.1	93/96	96.9	108/109	99.1	65/72	90.3
18	29/65	44.6	34/40	85.0	49/79	62.0	54/95	56.8	47/109	43.1	45/67	67.2
19	0/66	0	0/42	0	0/120	0	1/108	0.9	0/109	0	0/71	0
20	8/65	12.3	9/42	21.4	9/120	7.5	13/108	12.0	1/109	0.9	0/71	0
21	35/66	53.0	10/41	24.4	41/105	39.0	41/103	39.8	22/109	20.2	6/71	8.4

highest MU value corresponded to *A. sapidus*, and, to a lesser extent, to the semiaquatic morphotype of *A. terrestris* from Lugano; the lowest MUs appeared in the fossorial populations of this latter species from Nyon, Ally and Ribadesella (Tab. 2). The phenogram of distances constructed from the MMDs matrix (Fig. 3) showed that the Ebro Delta sample (*A. sapidus*) appeared clearly separated from the samples of *A. terrestris*. Within these latter, the specimens from the south of the Alps differed significantly from the cluster formed by the remaining samples, in which the animals from the Aran Valley were the most different phenetically. The samples from Nyon and Ally formed a cluster that was significantly separated from the sample from Ribadesella.

Table 2. Mean Measures of Divergence (MMDs) in six populations of *Arvicola* based on the frequencies of 15 nonmetric cranial traits (upper matrix), and standard deviation for each MMD (lower matrix). For each sample the Measure of Uniqueness (MU) was calculated. *A. terrestris*: Lugano, Nyon, Ally, Ribadesella (Ribad.) and Aran Valley (Aran V.); *A. sapidus*: Ebro Delta (Ebro D.).

Sample	Lugano	Nyon	Ally	Ribad.	Aran V.	Ebro D.	MU
Lugano	–	0.1279	0.2383	0.3075	0.3304	0.6073	1.6114
Nyon	0.0198	–	0.0384	0.1105	0.1034	0.5365	0.9167
Ally	0.0132	0.0194	–	0.0530	0.1081	0.5522	0.9900
Ribad.	0.0130	0.0173	0.0106	–	0.1841	0.3917	1.0468
Aran V.	0.0124	0.0167	0.0101	0.0099	–	0.6463	1.3723
Ebro D.	0.0149	0.0192	0.0125	0.0123	0.0118	–	2.7340

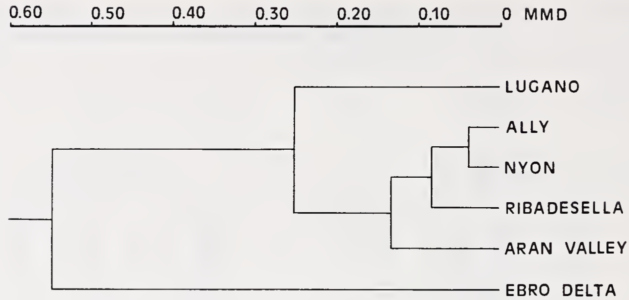

Fig. 3. Distance phenogram constructed from the MMDs obtained among six samples of *Arvicola* from southwestern Europe. *A. terrestris*: Lugano, Ally, Nyon, Ribadesella and Aran Valley; *A. sapidus*: Ebro Delta.

Discussion

The noticeable phenetic separation reported here between *A. sapidus* and *A. terrestris* coincides with the results given by Corbet et al. (1970), and thus the incidence of nonmetric cranial traits clearly agrees with the present taxonomic conception of the genus. Our results indicate that *A. sapidus* differs in general from all the samples of *A. terrestris* studied, and in particular, in the relatively high frequency of traits 6, 7 and 13, and the low incidence of trait 21. Comparing our data with the frequencies obtained by Corbet et al. (1970) for northern Spain *A. sapidus*, marked differences appear in traits 2, 4, 9 and 14. These differences are probably due to these traits being difficult to score objectively.

Among samples of *A. terrestris*, animals from Lugano are the most divergent in the incidence of nonmetric variants. These results are in accordance with the high genetic distance, deduced from gel electrophoresis data, between *A. t. italicus* and several semiaquatic and fossorial populations of the species (cf. Saucy et al. 1994) and, in particular, from the nearest fossorial populations of *A. t. scherman* from the north of the Alps (Graf 1982; Saucy et al. 1994). Based on the possible lack of gene flow between *italicus* and *scherman* (Graf 1982) and taking into account the mechanisms of reproductive isolation between them (Morel 1981), Graf (1982) suggested that both forms are on the way to becoming separate species. The high phenetic distance observed between our samples from Lugano and Nyon reaffirms the distinctiveness of *italicus* and *scherman*. In particular, from the variants used in the cluster analysis, the most conspicuous differences between the two forms appear in traits 5, 8, 10 and 21.

Although results of biochemical polymorphism have revealed a low level of genetic variability among fossorial populations of *A. terrestris* from southwestern Europe (Saucy et al. 1994), our results indicate significant variations among populations in the general incidence of nonmetric cranial traits. With respect to the data given by Corbet et al. (1970) for the specimens of *A. t. monticola* from the Pyrenees, our results corresponding to the sample from the Aran Valley also show noticeable differences in the frequencies of traits 4, 9 and 14, which might be due to the afore-mentioned subjective character of these variants.

Within the fossorial populations analysed, animals from western Switzerland and the Massif Central were phenetically similar, a result that coincides with their common subspecific status (cf. Morel 1981). On the other hand, both samples are more phenetically similar to the Cantabrian animals than to the Pyrenean ones. The general divergence in the incidence of the traits used in the comparative analyses (especially traits 11, 12 and 13) between animals from Cantabria and the Pyrenees support their different subspecific status (cf. Ventura and Gosálbez 1989; Ventura 1991).

The differences in frequencies of nonmetric cranial traits in southwestern European populations of *Arvicola* agree, in general, with our current understanding of the morphological, biometric, biochemical and reproductive relationships among several of these populations, and with their present taxonomic status. Therefore, we suggest that these traits can be considered useful for assessing genetic divergence among populations of this genus. Under this assumption, the results allow us to deduce new considerations on the genetic relationships between Iberian and French populations of *A. terrestris*. The significant phenetic divergences among the samples from the Pyrenees, Massif Central and northwestern Spain indicate the action of some barriers to gene flow. Available data on the geographic distribution of *A. terrestris* in France (cf. Baudoin 1984) and Spain (cf. Castién 1984; Álvarez et al. 1985; Ventura and Gosálbez 1988; Castién and Gosálbez 1993/94), suggest that the populations from the southwestern France departments of Lot and Garone, Gironde and Landes, and those from the Basque Country constitute fragmented groups of geographic populations (probably as shown in Fig. 1) representative of an earlier continuous distribution area, which connected the populations from the Cantabrian region, Pyrenees and southwestern and central France. The genetic drift accounts for at least some of the variability in nonmetric traits in both laboratory and wild populations (cf. Hartman 1980). Since population densities of the fossorial form of *A. terrestris* show multiannual fluctuations (cf. Saucy 1988), during troughs populations can pass through genetic bottlenecks, in which the genetic drift might especially act. This factor, together with the lack of gene flow because of geographic isolation, could have favoured the phenetic differentiation observed in the French and Spanish populations.

Acknowledgements

We are grateful to Dr. A. Meylan (Changins), Dr. E. L. Petavy (Lyon) and M. Braña (Oviedo) for the donation of the samples from Switzerland, the French Massif Central and Asturias, respectively. We thank Dr. J. B. Searle (York), Prof. Dr. J. Gosálbez and Dr. M. J. López-Fuster (Barcelona) for critical reading and constructive comments made on an earlier draft of this study. We also thank R. Rycroft (SAL, University of Barcelona) for improving the English text.

Zusammenfassung

Geographische Variation und Divergenz epigenetischer Schädelmerkmale bei Arvicola (Mammalia, Rodentia) in Südwesteuropa

Die geographische Variation und Divergenz von 21 nichtmetrischen Eigenschaften des Schädels wurde bei sechs *Arvicola*-Stichproben untersucht (*Arvicola terrestris*: Südosten und Westen der Schweiz, französisches Zentralmassiv, spanische Pyrenäen und Nordwesten Spaniens; *Arvicola sapidus*: Ebro Delta, Spanien). Die phänetische Distanz unter den Mustern wurde durch den mittleren Abweichungswert (MMD) ausgedrückt, der aus der Umwandlung der Charakterhäufigkeiten in Winkelwerte erhalten wurde. Ausgehend von den MMDs jedes Musters wurde mittels der UPGMA-Methode eine Gruppenanalyse erhoben. Im so erhaltenen Phänogramm der Abstände bildeten alle *A. terrestris* eine von *A. sapidus* getrennte Gruppe. In der ersten zeigte die Stichprobe aus dem Südosten der Schweiz die größte phänetische Abweichung gegenüber dem Rest der Gruppe. Innerhalb der iberischen Stichproben wurde ein größerer Grad an phänetischer Abweichung gemessen als zwischen den Exemplaren aus Nordwestspanien und denen aus dem Zentralmassiv und dem Westen der Schweiz. Die niedrigste Abweichung wurde zwischen den letztgenannten Stichproben beobachtet. Da die Resultate mit der allgemeinen Kenntnis über die morphologischen, biometrischen, biochemischen und reproduktiven Beziehungen zwischen den untersuchten Populationen übereinstimmen, kann man die nicht-metrischen Schädeleigenschaften als brauchbares Mittel zur Einschätzung der genetischen Differenzierung von Schermäusen und folglich zum Verständnis der phylogenetischen Beziehungen zwischen den Populatio-

nen bezeichnen. Unter dieser Annahme und in Anbetracht erhaltener Resultate können neue Hypothesen bezüglich der genetischen Beziehungen der Populationen im Zentrum Frankreichs, in den Pyrenäen und im Nordwesten Spaniens aufgestellt werden.

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